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Macroscopic approaches to root water uptake as a function of water and salinity stress

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ABSTRACT

Computer simulation models can be important tools for analyzing and managing site-specific irrigation, soil salinization, or crop production problems. For many of these problems, computer analyses require simulations of root water uptake as a function of water and salinity stress. We give an overview of macroscopic modeling approaches that are based on the Richards equation with a sink term specifying water uptake. Various parameterizations of the sink term as functions of water and salinity stress are reviewed. An example application demonstrates the simulation of drainage for a wide range of salinity and water stress conditions. The example shows that in practice it is very difficult to discriminate among the various functional forms proposed for the sink term. Future improvements to models may involve the incorporation of more dynamic root functions, such as the ability of roots to respond actively to growing conditions. As an example, we consider modeling compensated uptake, in which plants react to stress in one section of the root zone by increasing uptake in sections with more favorable conditions. Lastly, the challenge of estimating uptake reduction parameters from crop salt tolerance databases is discussed.

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1. Introduction

Irrigation has contributed significantly to increased crop production worldwide. Unfortunately, irrigation has contributed also to increased salinization of agricultural lands, and has caused the destruction of agriculture in many areas (Van Schilfgaarde, 1980, 1984, 1994). About 20–30 million ha of irrigated land are seriously damaged by the build-up of salts and 0.25–0.5 million ha are estimated to be lost from production every year as a result of salt build-up (FAO, 2002). The FAO/AGL SPUSH network (<http://www.fao.org/ag/agl/agll/spush/intro.htm>) estimates that 19.5% of the world's 230 million ha of irrigated land is salt-affected. In the United States, 9% of cropland and pastureland suffers from reduced productivity due to salinity (Ghassemi et al., 1995). Still, despite the negative impacts, irrigation is critical to sustaining

and increasing agricultural production. While about 17% of agricultural land worldwide is irrigated, this 17% accounts for about 40% of the total global food harvest (FAO, 2002). Moreover, per capita arable land has decreased over the years, from a worldwide average of 0.38 ha in 1970 to 0.28 ha in 1990, and some analysts project a further decrease to 0.15 ha in 2050 (Ghassemi et al., 1995). Hence, increased production must come from increased average yields, increases that will be possible only through high-yielding irrigated agriculture.

Effective management of salt-affected soils requires knowledge of many coupled physicochemical processes affecting soil conditions. Computer models such as SWAP (van Dam et al., 1997; Kroes and van Dam, 2003) and HYDRUS-1D (Šimunek et al., 2005) have become increasingly important tools for analyzing site-specific irrigation, soil salinization, or crop production problems. Most of these models are based on

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the Richards equation for variably saturated water flow and the advection–dispersion equation for solute transport. In their simplest one-dimensional forms, these equations are

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial z} \left[K(h) \frac{\partial h}{\partial z} - K(h) \right] - S \quad (1)$$

$$\frac{\partial (\theta Rc)}{\partial t} = \frac{\partial}{\partial z} \left(\theta D \frac{\partial c}{\partial z} - qc \right) - \phi \quad (2)$$

respectively, where θ is the volumetric water content, h the soil water pressure head (L), t the time (T), z the depth (L), K the hydraulic conductivity (L T⁻¹), R a retardation factor accounting for sorption or exchange, c the solute concentration of the liquid phase (M L⁻³), D the solute dispersion coefficient (L² T⁻¹), q the Darcy–Buckingham volumetric water flux (L T⁻¹), and S (T⁻¹) and ϕ (M L⁻³ T⁻¹) are sinks or sources for water and solutes, respectively. In this paper, S and ϕ are associated exclusively with root uptake processes.

While models based on Eqs. (1) and (2) are critical tools in irrigation and drainage studies, the equations pose challenges because of (i) the many highly nonlinear processes involved, including water and energy exchange between the biosphere and the atmosphere; (ii) issues of scale, especially for studies at larger field and watershed scales; (iii) lack of data on the many parameters required in the model. Proper parameterization of root water uptake as a function of water and salinity stress remains one of those challenges.

A large number of microscopic and macroscopic approaches to modeling water uptake have been proposed over the years. Comprehensive reviews from a mostly hydrological perspective include Molz (1981), Hopmans and Bristow (2002), Wang and Smith (2004), and Feddes and Raats (2004). The microscopic approach generally involves descriptions of radial flow to, and uptake by, individual roots (Hillel et al., 1975; Raats, in press). In contrast, modeling uptake with a sink term in the Richards equation (Eq. (1)) is a typical macroscopic approach that averages uptake over a large number of roots. The approach ignores or implicitly averages pore-scale variations in the pressure head or solute concentration in the immediate vicinity of individual roots.

This paper is limited to the macroscopic approach. Specifically, we review relatively standard macroscopic approaches to modeling root water uptake in the presence of water and salinity stress, provide an example application involving a lysimeter study, briefly raise the issue of compensatory uptake, and discuss some practical issues concerning the use of salt tolerance databases to determine uptake reduction parameters. Elsewhere in this issue, Green et al. (this issue) provide an overview of root uptake that is complimentary to our discussion, focusing on new technologies for measuring plant water use and observing compensatory uptake, and on the use of modeling to develop better irrigation policies for allocating water.

2. General model for the root water uptake term

The root water uptake term S in Eq. (1) should in general be a function of the soil water pressure head, the osmotic pressure

head, root characteristics, and meteorological conditions such as evaporative demand. Several approximations have been used for S in the macroscopic approach. A popular early approach assumed that uptake rate is proportional to the difference between the soil water pressure head, h , and an effective root water or plant pressure head (or potential), h_r , leading to the general form:

$$S(z) = b(z)(h - h_r) \quad (3)$$

in which b is a function that has been hypothesized in various studies to depend on depth (z), the local average soil water pressure head (h), the soil water content (θ), the soil hydraulic conductivity ($K(h)$), soil and plant (xylem) resistances to root water uptake, and/or the root distribution versus depth (e.g., Hillel et al., 1976; Molz, 1981). One version of Eq. (3) that has been used in many numerical simulations is (Whisler et al., 1968; Bresler et al., 1982):

$$S(z) = b(z)K(h)(h - h_r) \quad (4)$$

in which b is now a depth dependent proportionality constant, often referred to as the root effectiveness function (L⁻²). Some studies (e.g., Feddes et al., 1974) have used a term corresponding to $1/b(z)$ rather than $b(z)$ in Eq. (4), while others accounted for gravity by substituting the hydraulic head for the pressure head (e.g., Gardner, 1964). Although $b(z)$ is essentially an empirical parameter that somehow integrates the physics of flow at and across the soil–root interface, in practice $b(z)$ has been assumed to reflect the relative root distribution in the soil profile, and as such has been equated to the normalized root density function with units of root length per unit volume of soil (Whisler et al., 1968). Most studies assumed that h_r in Eq. (2) or (3) is constant over the root zone. The value of h_r generally depends on specific soil, plant, and climatic conditions, and cannot become less than some critical value, h_{cr} , commonly taken to be the permanent wilting point (–150 m). Once S is calculated as part of a numerical solution of Eqs. (1) and (4), the transpiration rate, T_a , may be calculated with

$$T_a = \int_{L_R} S dz \quad (5)$$

where L_R is the depth of the root zone.

Eq. (3) describes water uptake as a function of water stress only. Bresler et al. (1982), among others, accounted for salinity stress by adding the osmotic head, π , directly to the pressure head:

$$S(z) = b(z)K(h)(h + \pi - h_r) \quad (6)$$

thus implying simple additivity of water and salinity contributions to plant stress. Again, Eq. (6) may be modified to account for the effects of gravity by substituting the hydraulic head for the pressure head (e.g., Childs and Hanks, 1975). Eqs. (4) and (6) have been shown to work very well for non-saline or mildly saline conditions, but not necessarily for more saline situations. For example, Cardon and Letey (1992a,b) showed that Eq. (6) may lead to unreasonable

shifts between optimal and zero transpiration as compared to experimental data. Because of the dominance of the hydraulic conductivity term, Eq. (6) failed to predict significant decreases in transpiration under highly saline conditions.

As an alternative to Eq. (4), Feddes et al. (1978) and Belmans et al. (1983) suggested a much simpler root extraction term that depends only on the pressure head and a maximum or potential transpiration rate:

$$S(z) = \beta(z)\alpha(h)T_p \quad (7)$$

where $\beta(z)$ is the normalized root density distribution (L^{-1}), T_p the potential transpiration rate ($L^3 L^{-2} T^{-1}$), and $\alpha(h)$ is a dimensionless water stress response function, sometimes called the uptake reduction function ($0 \leq \alpha \leq 1$). Note that under conditions of no stress, $\alpha = 1$ and Eq. (7) reduces to

$$S_p(z) = \beta(z)T_p \quad (8)$$

where S_p (T^{-1}) is the potential uptake rate. A large number of functions for $\beta(z)$ have been proposed and used, including constant, linearly decreasing, trapezoidal, and exponential functions. We refer the reader to Hoffman and Van Genuchten (1983) and Hao et al. (2005) for details.

In the sections below we discuss various functional forms for the water stress response function (Section 3.1), equivalent formulations for salinity stress (Section 3.2), and possible ways of combining water and salinity stress using these functions (Section 3.3).

3. Uptake reduction models for water and salinity stress

Eq. (7) defines a very general equation for the effects of drought stress on water uptake. Similar forms can be postulated for salinity stress (or for any other variable such as nutrient stress), i.e.:

$$S(z) = \beta(z)\alpha(\pi)T_p \quad (9)$$

One important question is how to combine water and salinity stress. That question is discussed in Section 3.3. We focus first on reduction functions for water stress (Section 3.1) and salinity stress (Section 3.2) separately.

Many of the functional forms that have been proposed for uptake reduction are patterned after whole-plant water use and salt stress relationships. This correspondence is motivated by the often assumed relationship (De Wit, 1958; Doorenbos and Kassam, 1979):

$$\frac{Y}{Y_p} = \frac{T_a}{T_p} = \alpha \quad (10)$$

where Y is the yield and Y_p is the potential yield (i.e., the maximum yield that would be obtained under optimal growing conditions). Pertinent examples of whole-plant response functions include the threshold-slope model of

crop yield response to soil salinity (Maas and Hoffman, 1977):

$$\frac{Y}{Y_p} (\%) = \begin{cases} 100, & EC_e \leq A \\ 100 - B(EC_e - A), & A < EC_e \leq \frac{100}{B} + A \\ 0, & EC_e > \frac{100}{B} + A \end{cases} \quad (11)$$

and the S-shaped salinity yield response curve (van Genuchten and Hoffman, 1984):

$$\frac{Y}{Y_p} = \frac{1}{1 + \left(\frac{C}{C_{50}}\right)^p} \quad (12)$$

In Eqs. (11) and (12), EC_e ($dS m^{-1}$) is the root-zone-averaged saturation extract electrical conductivity, A ($dS m^{-1}$) and B ($\% m dS^{-1}$) the empirical parameters called the threshold salinity and slope parameters, respectively, C the average root zone salt concentration, and p and C_{50} are the empirical parameters, the latter corresponding to the salt concentration at which yield is reduced by half. The exponent p was found to be approximately 3 when Eq. (12) was applied to a large number of crop salt tolerance data sets (van Genuchten, 1987; van Genuchten and Gupta, 1993). Eq. (12) has been successfully fitted to salt tolerance data for many crops (van Genuchten and Gupta, 1993; Steppuhn et al., 2005a, b).

3.1. Water stress response functions

Feddes and Raats (2004) reviewed various functional forms for α that have been proposed over the years. We mention here two general model types that have been used most often: piecewise linear functions and continuous smooth functions. To describe water stress, Feddes et al. (1978) proposed a piecewise linear reduction function parameterized by four critical values of the water pressure head, $h_4 < h_3 < h_2 < h_1$:

$$\alpha(h) = \begin{cases} \frac{h - h_4}{h_3 - h_4}, & h_3 > h > h_4 \\ 1, & h_2 \geq h \geq h_3 \\ \frac{h - h_1}{h_2 - h_1}, & h_1 > h > h_2 \\ 0, & h \leq h_4 \text{ or } h \geq h_1 \end{cases} \quad (13)$$

Fig. 1a shows a plot of Eq. (13). Note that in this model water uptake is reduced at high and low water contents. Uptake is at the potential rate when the pressure head is $h_3 \leq h \leq h_2$, drops off linearly when $h > h_2$ or $h < h_3$, and becomes zero when $h \leq h_4$ or $h \geq h_1$. In general, the value of h_3 is expected to be a function of evaporative demand.

van Genuchten (1987) proposed an alternative smooth, S-shaped reduction function to account for water stress:

$$\alpha(h) = \frac{1}{1 + \left(\frac{h}{h_{50}}\right)^{p_1}} \quad (14)$$

where h_{50} and p_1 are adjustable parameters (Fig. 1b). Eq. (14) was motivated by a study (van Genuchten and Hoffman, 1984) that found that an S-shaped function (Eq. (12)) described salt tolerance yield reduction data better than other functions, including the threshold-slope model of

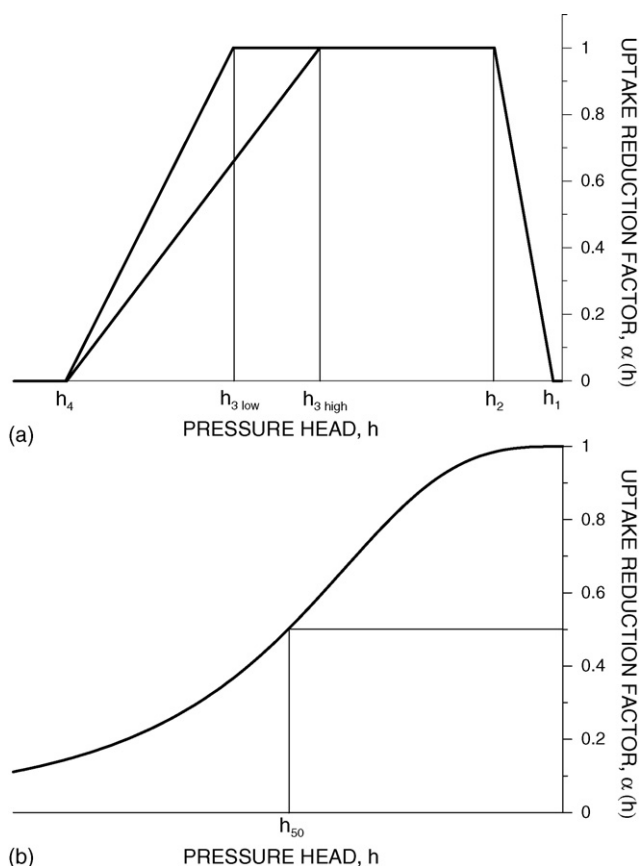


Fig. 1 – Plots of (a) the Feddes et al. (1978) water stress uptake reduction function (Eq. (13)), and (b) the S-shaped function of van Genuchten (1987) (Eq. (14)).

Maas and Hoffman (1977). van Genuchten (1987) reasoned that if water and salinity stress are assumed to have similar effects on yield, and hence on transpiration, then the S-shaped function should also be applicable to water stress response data.

3.2. Salinity stress response functions

Consistent with the Maas and Hoffman (1977) model for crop salt tolerance (Eq. (11)), the effects of salinity stress on root water uptake can be described using the piecewise linear (threshold-slope) function:

$$\alpha(\pi) = \begin{cases} 1, & a \leq \pi \leq 0 \\ 1 + b(\pi - a), & a > \pi > a - \frac{1}{b} \\ 0, & \pi \leq a - \frac{1}{b} \end{cases} \quad (15)$$

where a and b are the adjustable parameters, often referred to as the salinity threshold and slope, respectively, thus mirroring the terminology used for the Maas-Hoffman parameters A and B . Note, however, that the parameter sets are not the same: A and B parameterize total yield reductions as a function of average root zone salinity, whereas a and b parameterize local reductions in the root water uptake rate as a function of osmotic head.

Similarly, in correspondence to Eq. (12), a smooth function may be postulated for the effects of salinity stress on local root water uptake:

$$\alpha(\pi) = \frac{1}{1 + \left(\frac{\pi}{\pi_{50}}\right)^{p_2}} \quad (16)$$

where p_2 and π_{50} are the adjustable parameters, the latter being the osmotic pressure head where uptake is halved.

3.3. Combined water and salinity stress

A major challenge is how to combine the effects of water and salinity stress. Uptake reductions due to a combination of water and salinity stresses could be modeled by assuming that the stresses are somehow additive or multiplicative. A generalized model for additive stresses is obtained by assuming that water uptake occurs in response to some weighted sum of the soil water pressure and osmotic heads:

$$\alpha(h, \pi) = \frac{1}{1 + \left[\frac{a_1 h + a_2 \pi}{\pi_{50}}\right]^{p_2}} \quad (17)$$

with simple additivity resulting when $a_1 = a_2 = 1$. Although additivity has been inferred from a number of laboratory and field experiments (e.g., Wadleigh, 1946; Meiri and Shalhevet, 1973; Childs and Hanks, 1975; du Plessis, 1985; Bresler and Hoffman, 1986), its general applicability remains uncertain (Shalhevet and Hsiao, 1986), especially for field conditions subject to relatively wide ranges in pressure heads (wetting/drying cycles).

Linear or weighted additivity is only one of several possibilities for combining the effects of water and salinity stress. Another approach presumes that water and salinity effects are multiplicative. In the general case this leads to

$$\alpha(h, \pi) = \alpha(h)\alpha(\pi) \quad (18)$$

where $\alpha(h)$ and $\alpha(\pi)$ can be any of the functions in Sections 3.1 and 3.2. For example, if Eqs. (14) and (16) are used, this gives

$$\alpha(h, \pi) = \frac{1}{1 + \left(\frac{h}{h_{50}}\right)^{p_1}} \frac{1}{1 + \left(\frac{\pi}{\pi_{50}}\right)^{p_2}} \quad (19)$$

where h_{50} , π_{50} , p_1 and p_2 are the presumably crop, soil, and climate-specific parameters.

4. An application

In practice, it is difficult to determine which of the reduction functions (those noted here as well as others, reviewed for example by Feddes and Raats (2004)) best describes root water uptake. The detailed root zone and transpiration data needed to discriminate the models are difficult to obtain and rarely available. We illustrate this using data from a recent experiment (Skaggs et al., 2006a, 2006b) conducted in a lysimeter facility consisting of 24 volumetric lysimeters, each measuring 81.5 cm wide \times 202.5 cm long \times 85 cm deep. The lysimeters were filled with river sand (96% sand, 3% silt, 1%

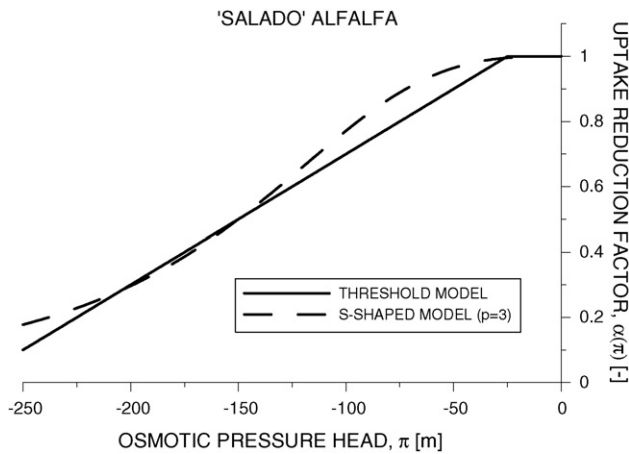


Fig. 2 – Comparison of the threshold-slope salinity stress reduction function used by Skaggs et al. (2006b) (solid line) and the S-shaped function (dashed line) used in the simulations presented in Figs. 3 and 4.

clay) to a depth of 80 cm. Twelve of the lysimeters were planted with ‘Salado’ alfalfa (*Medicago sativa*) and 12 with ‘Jose’ tall wheatgrass (*Agropyron elongatum*). The crops were established over several months using low salinity irrigation water.

Experimental treatments started on 2 May 2002 (day of year 122) and proceeded in two phases. During the first phase (DOY 122–237) only salinity stress was imposed, with all lysimeters being abundantly irrigated with waters ranging in salinity from 2.5 to 28 dS m⁻¹. The second phase (DOY 247–297)

involved a combination of salinity and drought stresses; the same irrigation waters were used, but the lysimeters were irrigated with a prescribed fraction ($f = 0.5, 0.75, 1.0, \text{ or } 1.25$) of water consumed in two well-watered “control” lysimeters. Thus, lysimeters with $f < 1$ received less water than was being consumed in the control, whereas lysimeters with $f \geq 1$ received water equal to or in excess of that amount. During both phases the lysimeters were irrigated every other day. Drainage was measured nearly continuously throughout the experiment.

Skaggs et al. (2006b) simulated the experiment using HYDRUS-1D (Šimunek et al., 2005) with a reduction function that combined Eqs. (14) and (15) into a multiplicative model:

$$\alpha(h, \pi) = \frac{1}{1 + \left(\frac{h}{h_{50}}\right)^{p_1}} [1 + b(\pi - a)] \tag{20}$$

Using a trial-and-error fitting procedure, Skaggs et al. (2006b) obtained values for h_{50} , p_1 , a , and b which resulted in the simulated drainage being in very good agreement with the measured drainage. However, due to complications arising from the coarseness of the sandy soil, they found that the modeling results were mostly insensitive to the form of the water stress component of the reduction factor, and thus were unable to evaluate the performance of the S-shaped water stress response function and the assumed multiplicative interaction.

We have now re-analyzed their alfalfa drainage data to show that a comparable fit to the data could have been obtained using the S-shaped function for the salinity reduction (i.e., Eq. (16)) instead of the threshold-slope model in Eq. (20). Skaggs et al.

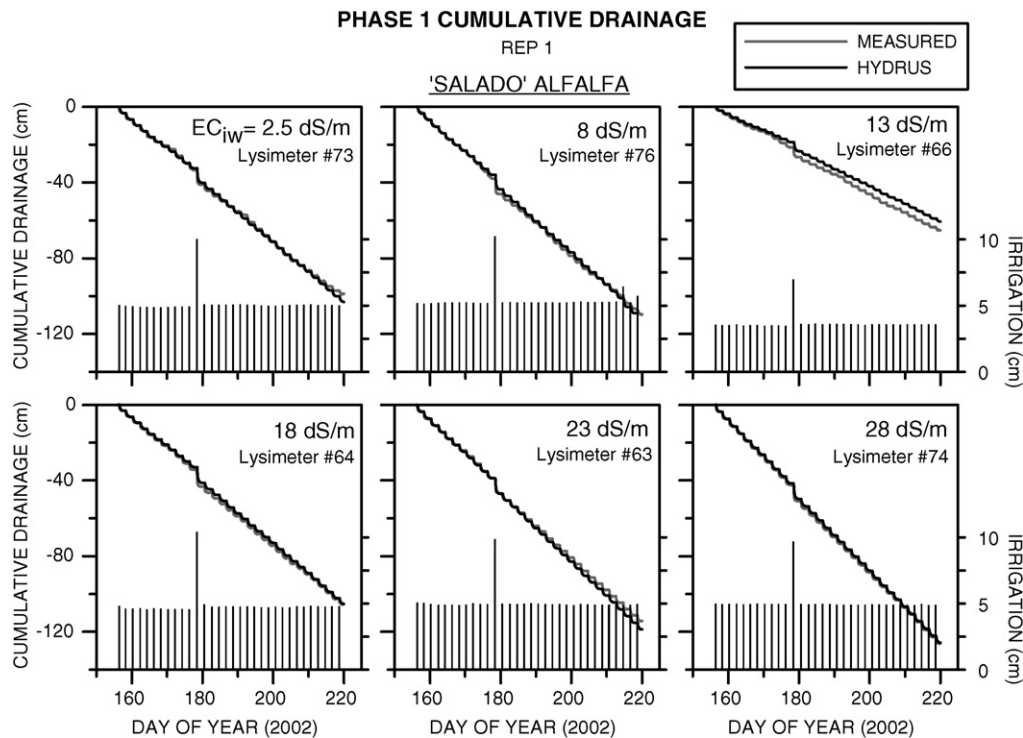


Fig. 3 – Comparison of simulated cumulative drainage with that measured during the “Phase 1” experiments of Skaggs et al. (2006a, 2006b). Text in each plot indicates the irrigation water salinity (EC_{iw}) and the lysimeter number. Irrigation timings are shown on the bottom of each plot and the irrigation depth is indicated on the axes on the right side of each plot.

(2006b) used the values $a = -25$ m and $b = 0.004 \text{ m}^{-1}$ in the threshold model. For the S-shaped model we used $p_2 = 3$ (the value recommended by Šimunek et al. (2005) based on the aforementioned $p = 3$ value obtained by van Genuchten (1987)) and $\pi_{50} = -150$ m (the value of π corresponding to $\alpha = 0.5$ in the threshold model used by Skaggs et al. (2006b)). As shown in Fig. 2, the threshold model used by Skaggs et al. (2006b) and the S-shaped model used here nearly coincide.

Figs. 3 and 4 present plots of cumulative drainage simulated using the S-shaped function as well as the drainage

measured by Skaggs et al. (2006a). The agreement between the data and simulations shown in Figs. 3 and 4 is essentially the same as reported by Skaggs et al. (2006b) for the threshold model (results not shown here), with both approaches (i.e., Eqs. (19) and (20)) producing a close match with the data.

The Skaggs et al. (2006a) experiment was not ideal for identifying the full uptake reduction function since the coarse soil texture was ill-suited for studying the drought response. Still, the experiment did allow for a good examination of the salinity response function. However, the drainage data were

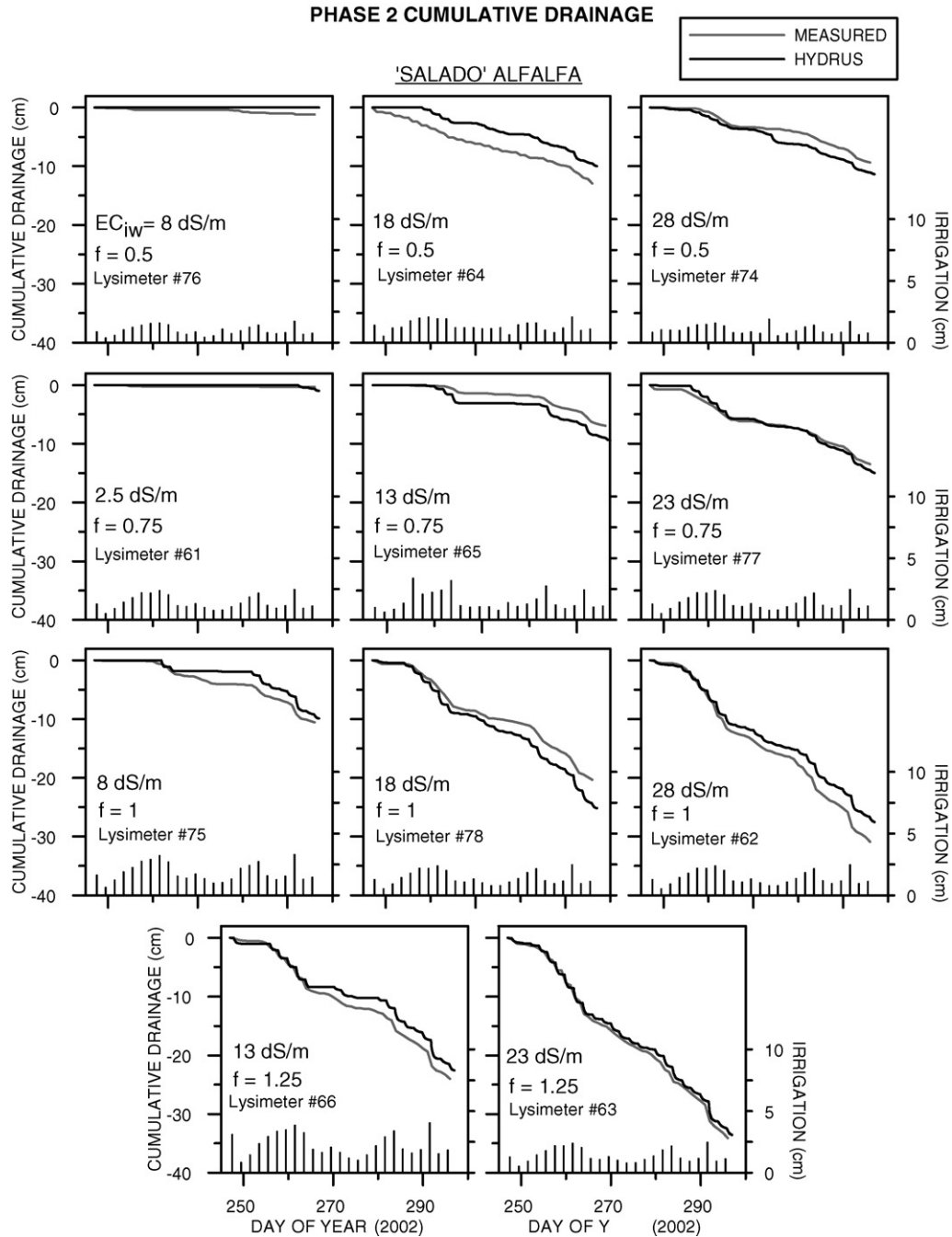


Fig. 4 – Comparison of simulated cumulative drainage with that measured during the “Phase 2” experiments of Skaggs et al. (2006a, 2006b). Text in each plot indicates the irrigation water salinity (EC_{iw}), the target irrigation depth f , and the lysimeter number (see text for an explanation of f). Irrigation timings are shown on the bottom of each plot and the irrigation depth is indicated on the axes on the right side of each plot.

not sufficient to discriminate between the S-shaped and the threshold–slope models—either model could describe the data equally well. In general, we suspect that drainage data or transpiration data (or a surrogate such as yield data) alone will not permit discriminating among different functional forms for reduction functions such as those considered here, as well as others containing additional parameters (e.g., Homae et al., 2002a; Dudley and Shani, 2003; Feddes and Raats, 2004). Additional detailed root zone data might allow for discrimination; Green et al. (this issue) discuss measurement technologies that may provide such data. However, our view is that most of the proposed reduction models can be calibrated to produce essentially the same simulation results, at least within the limits of experimental observation.

Finally, we emphasize that the reduction function approach used in hydrologically oriented uptake models as reviewed here has a limited plant physiological basis. For example, it is known that plant response to salinity stress may not be constant over time: osmotic effects tend to dominate initially, whereas over the long term the accumulation of ions may become more important (Munns, 2002). This latter effect, plus other temporal components of plant response, is not accounted for in the type of models considered here. On balance, we think that further refinement of the functional forms of the reduction functions is not warranted at this time, and recommend the use of the two-parameter S-shaped models (Eqs. (14) and (16)) which provide sufficient flexibility without the introduction of unwarranted complexity.

5. Compensated water uptake

One area of research that may improve hydrologically oriented models of root water uptake involves the development of sink terms which incorporate a wider range of dynamic root and plant function. As biological organisms, plants and roots may respond in various ways to environmental stresses. Of interest are root functions that could be represented without having to model plant physiology in detail. One example is compensated water uptake in which plants may respond to non-uniform stress conditions by increasing water uptake from sections of the root zone with more favorable conditions (Taylor and Klepper, 1978; Hasegawa and Yoshida, 1982; Jarvis, 1989).

Compensatory water uptake is potentially an important aspect of irrigation and drainage practices that impose nonuniform water stress in the root zone. These practices include deficit irrigation (e.g., English and Raja, 1996; Leib et al., 2006), partial root zone drying (e.g., Kang et al., 2002; Stikic et al., 2003), and deficit irrigation in combination with shallow groundwater management (e.g., Ayars et al., 1999; Shouse et al., 2006). Since these practices rely on the ability of a crop to respond to stress, including compensatory uptake in models of root water uptake would clearly aid in the analysis and design of such practices.

Several modeling approaches are possible for compensatory water uptake (e.g., Li et al., 2001; Braud et al., 2005). We briefly review here the approach of Jarvis (1989), as modified by Šimunek et al. (2005) in HYDRUS-1D. Jarvis (1989) formulated the following in terms of the soil water content, whereas

Šimunek et al. (2005) used the soil water pressure head as the controlling variable.

First recall that for the models in Section 3.1, the actual transpiration rate T_a is given by

$$T_a = T_p \int_{L_R} \alpha[h(z)]\beta(z) dz \quad (21)$$

where as before T_p is the potential transpiration rate, α the water stress reduction factor, and $\beta(z)$ is the normalized root density distribution. To formulate a compensatory uptake model, define ω to be

$$\omega \equiv \int_{L_R} \alpha[h(z)]\beta(z) dz \quad (22)$$

Note that $0 \leq \omega \leq 1$. The functional ω is called the weighted stress index and provides a measure of total plant stress, with $\omega = 1$ indicating no stress throughout the soil root zone.

The transpiration rate for compensatory water uptake is now given by

$$\frac{T_a}{T_p} = \begin{cases} 1, & \omega_c < \omega \leq 1 \\ \frac{\omega}{\omega_c}, & \omega < \omega_c \end{cases} \quad (23)$$

where $0 < \omega_c \leq 1$. According to this formulation, transpiration occurs at the potential rate ($T_a = T_p$) when the total stress is relatively low (i.e., when ω is greater than some critical value ω_c). To obtain the potential rate, uptake is increased throughout the root zone by a factor of $1/\omega$. Although on a relative basis uptake is increased uniformly throughout the root zone, in absolute terms the biggest increase occurs in those parts of the root zone where stress is low and/or the root density is high (i.e., where $S(z) = \alpha[h(z)]\beta(z)$ is large). Conversely, the increase is negligible in sections where $S(z)$ is very small. Root water uptake from stressed parts of the root zone is hence fully compensated by uptake from other parts. When stress is higher and $\omega < \omega_c$, compensation is only partial, with uptake increased throughout the root zone by a factor of $1/\omega_c$.

Unfortunately, little is known about the parameter ω_c . Jarvis (1989) analyzed oat, spring rape, and mustard crop data from a field experiment in Sweden and obtained a seemingly very low value of $\omega_c = 0.1$, implying fully compensated uptake except at very high levels of stress. The compensated uptake model also appears to have conceptual limitations. For example, let us assume momentarily that $\alpha[h(z)]$ is given by Eq. (14), the root distribution is uniform with depth ($\beta(z) = 1/L_R$), and the soil is initially at field capacity, uniformly wetted in the root zone. In that case $h(z) = h$ and, from Eq. (22), $\omega = \alpha(h)$. As the roots extract water from the soil, the soil would dry down uniformly, thus decreasing the value of $\alpha(h)$. As long as $\alpha(h) > \omega_c$, uptake would remain at potential levels and above the rate specified by $\alpha(h)$, with uptake being increased uniformly throughout the root zone by a factor of $1/\alpha$. Later when $\alpha(h)$ decreased below ω_c , uptake would fall below potential levels, although uptake throughout the root zone would still be greater by a factor of $1/\omega_c$ than the rate specified by $\alpha(h)$. However, both of these increases in uptake above the level specified by $\alpha(h)$ do not mimic compensatory uptake, and both seem to contradict the meaning of $\alpha(h)$. What, after all,

does $\alpha(h)$ stand for if it does not describe the reduction in uptake that occurs in this example? So while the model is capable of exhibiting compensatory behavior for certain types of stress conditions, it does not seem to be a completely satisfactory solution to the compensatory uptake problem either.

6. Estimation of uptake parameters from databases

Uptake reduction functions such as those given in Figs. 1 and 2 are generally very difficult to determine experimentally. We noted earlier that the various forms for the uptake reduction functions are similar to, and sometimes based on, forms that have been observed for whole-plant responses to stress. Because of this similarity, it has been anticipated (e.g., van Genuchten, 1987; van Dam et al., 1997) that uptake reduction parameters for different crops could be derived from literature studies of whole plant response. For example, Kroes and van Dam (2003, Appendix 3) provide a database of high and low h_3 parameters for the water stress reduction function given by Eq. (13), based on whole-plant observations compiled by Taylor and Ashcroft (1972).

An abundance of data exists for whole-plant salt tolerance as a function of root-zone-average salinity. Salt tolerance data may be found in Maas and Hoffman (1977), Maas (1990), and Steppuhn et al. (2005b), among other publications. In addition to using salt tolerance data to derive salinity uptake reduction parameters, van Genuchten (1987) noted the intriguing possibility of also deriving information about water stress parameters. If one assumes that water and salinity stress effects on the transpiration rate are approximately similar, then crop salt tolerance data could possibly be used to indirectly derive information about the water stress response function parameters. Eq. (17) is noteworthy in this regard as it expresses the combined drought and salinity uptake reduction in terms of the salinity reduction parameters π_{50} and p_2 . Thus, if π_{50} and p_2 were estimated from salt tolerance data, the uptake reduction due to water stress could be subsequently simulated with Eq. (17). Although Munns (2002) notes that at early times plant responses to water and salinity stresses are in fact similar, the appropriateness of water stress parameters obtained in this way is yet to be tested.

In any event, there are a number of potential problems that should be kept in mind when using plant salt tolerance data to derive parameter values for the salinity, water, and combined uptake reduction functions. One difficulty concerns the nature and quality of plant salt tolerance information, which most often has been reported in terms of the A and B parameters in Eq. (11). Maas and Hoffman (1977) themselves noted that “These data serve only as a guideline to relative tolerances among crops. Absolute tolerances vary, depending on climate, soil conditions, and cultural practices”. Additionally, the experimental data from which the tabulations of A and B were derived were very often not sufficient to determine salt tolerance parameters with great precision (e.g., van Genuchten and Gupta, 1993). Confidence intervals for A and B are typically not reported. Hence, while thousands of publications of crop salt tolerance studies have been compiled and indexed

(e.g., Francois and Maas, 1978, 1984), the data have been of limited value for many applications. Also, many salt tolerance studies failed to control or report environmental and cultural factors known to affect yield. Other experiments were conducted over a range of salinities that proved to be too narrow or too broad. All of this motivated Ulery et al. (1998) to advocate the development of a comprehensive computerized database of crop salt tolerance information that would permit a more effective evaluation of past work and, ultimately, more reliable estimates of the effects of environmental factors and cultural, soil, and water management practices on crop salt tolerance. Obtaining root water uptake information of the type discussed in this paper would certainly fall within the realm of possible applications of such a database.

A second difficulty is that the parameters A and B in Eq. (11) express plant salt tolerance as a function of a time and root-zone-averaged soil salinity (EC_e), whereas uptake reduction functions are parameterized in terms of the local osmotic and/or soil water pressure head. Thus, to derive uptake reductions parameters (e.g., a and b in Eq. (15)) from reported values of A and B , one must assume that the response to salinity stress at any point and time in the soil root zone is the same as the time-and-root-zone-integrated response by the entire plant or crop. This cannot be formally correct because of nonlinear dependencies of uptake on the pressure head or osmotic head, and also because of potentially significant effects of compensatory uptake. It is not clear what types of errors are introduced by equating local and global plant responses. Furthermore, converting A and B to a and b requires converting root-zone-average EC_e to π . In this context it should be remembered EC_e is the electrical conductivity of the saturation extract, not the conductivity of soil water. Recent studies by Homaei et al. (2002a,b,c) and Skaggs et al. (2006a, 2006b) demonstrate the various approximations needed to make the conversion, and show that uptake reduction parameters derived from salt tolerance data may in fact not produce accurate simulations. These conversion issues are discussed in detail by Ulery et al. (1998).

7. Concluding remarks

In this paper we gave an overview of macroscopic modeling approaches for root water uptake as a function of water and salinity stress. We showed that, at least for one set of lysimeter experiments involving a wide range of salinity and water stress conditions, it is very difficult to discriminate among alternative functional forms for the sink term. Future improvements to root water uptake models may involve the incorporation of more dynamic root functions, such as the ability of roots to respond actively to growing conditions. As an example, we considered compensated water uptake in which a plant reacts to stress in one part of the root zone by increasing uptake in other parts with more favorable conditions. We also discussed the challenge of estimating uptake reduction parameters from databases of whole-plant response, especially crop salt tolerance databases. Crop salt tolerance information is abundant in the literature but the accuracy of many of the data is questionable. In general, the data does not include information about soil and environmental factors and

cultural and water management practices known to affect crop salt tolerance and, indirectly, root water uptake. To derive uptake reduction parameters from whole-plant response data one must assume that the response to salinity stress at any point and time in the soil root zone is the same as the time-and-root-zone-integrated response by the entire plant or crop. This assumption cannot be formally correct because of the nonlinear nature of uptake processes, and neglects potentially significant compensatory uptake mechanisms. If uptake compensation played a role in many of the experiments used to construct plant water stress and salt tolerance databases, then estimates of $\alpha(h, \pi)$ from those databases would tend to be too high; including compensatory uptake in simulations would then account twice for the same mechanism (globally, not locally). Clearly, more research is needed in this area if we ever hope to use whole-plant response databases to parameterize uptake reduction functions and employ simulation models as predictive tools that do not require extensive crop- and site-specific calibration exercises involving inverse modeling (Hupet et al., 2003) or other methods of adjusting parameters (Skaggs et al., 2006b).

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